Azara's owl monkeys in the Humid Chaco: Primatological long-term studies in Argentina.

AZARA'S OWL MONKEY IN THE HUMID CHACO: PRIMATOLOGICAL LONG-TERM STUDIES IN ARGENTINA.

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ABSTRACT

The Owl Monkey Project started in 1996 as a multi-disciplinary program on the Azara's owl monkey of the Argentinean Chaco. The main goals of the project have been to investigate the evolution of the monogamous mating system and parental care of this species. The project has expanded and for many years we have also been exploring the potential relationship between demography, the spatial and temporal distribution of food resources and the monogamous social organization of the species. Additionaly since 2007, we expanded our studies to include the examination of groups that inhabit two different natural habitat types in the humid Chaco of Formosa Province. In this chapter, we use l data from 20 years to study, to elucidate factors underlying the demographic structure of different owl monkey groups inhabiting different types of habitats. The study is conducted in the Estancia Guaycolec (a 25,000 ha private cattle ranch) and in the National Park Rio Pilcomayo (a 52,000 ha protected area). In each study area, two sub-sets of owl monkey groups could be identified: within the gallery forests (continuous habitat), and groups in forest patches, as well as two potentially different levels of disturbance (i.e., national park, vs. cattle ranch). Our results confirm that the estimated densities for the private ranch are higher than in the National Park. In contrast, parameters like the size groups, birth rates and age structure were similar between sites. Group sizes, birth rates, and specific densities were larger for gallery forests than for forest island at both study sites. We found similarities in birth rates between different habitat types in the National Park, and in age structure at both study sites. Our studies not only contributes to the understanding of the evolution of social monogamy and male care, but also provides information on the demography and habitat use of a species that has been declared a Natural Monument.

RESUMEN

En el año 1996 comenzó el Proyecto Mirikiná, un programa de investigación multidisciplinario con los monos del género *Aotus* del Chaco argentino. El objetivo a largo plazo de este proyecto es comprender cuales son los mecanismos que mantienen la monogamia social y la importancia del cuidado parental en esta especie. El proyecto se ha ampliado y ya hace muchos años que hemos comenzado a explorar la relación entre la demografía, la distribución espacial y temporal de los recursos alimenticios y la organización social monógama de la especie. También, desde el 2007, hemos expandido nuestros estudios para agregar investigaciones de grupos que habitan dos tipos de hábitats naturales pero diferentes en el Chaco húmedo de la provincia de Formosa. En este capítulo presentamos datos de 20 años de estudio, que permiten dilucidar los factores que subyacen a la estructura demográfica de los diferentes grupos de monos mirikiná que habitan diferentes tipos de hábitats. El estudio se llevó a cabo en la Estancia Guaycolec (una estancia ganadera y privada de 25.000 ha) y en el Parque Nacional Río Pilcomayo (un área natural protegida de 52.000 ha). En cada área de estudio, dos sub-conjuntos de grupos de mirikinás pudieron ser identificados: dentro de las selvas en galería (hábitat continuo), y grupos sociales en islas de bosques, así como dos niveles potencialmente diferentes de perturbación (es decir un parque nacional vs. un establecimiento ganadero). Nuestros resultados confirman que las densidades estimadas para la estancia privada son más altos que en el Parque Nacional. En contraste, parámetros como el tamaño de los grupos, las tasas de natalidad y la estructura de edad fueron similares entre los sitios. El tamaño del grupo, las tasas de natalidad y densidades específicas fueron más altas en selvas en galería que en isletas de bosques para ambos sitios de estudio. Encontramos similitudes en las tasas de natalidad entre los diferentes tipos de hábitat en el Parque Nacional, y en la estructura de edades en ambos sitios estudiados. Nuestros estudios a largo plazo no sólo contribuyen a la comprensión de la evolución de la monogamia social y el cuidado paternal, sino que también proporcionan información importante sobre la demografía

y el uso del hábitat de una especie que ha sido declarada Monumento Natural en la Provincia de Formosa.

INTRODUCTION

General aspects of the genus Aotus

Individuals of the genus *Aotus* are characterized by two distinctive traits: they are the only anthropoid primates that are nocturnal and they are socially monogamous. *Aotus (Illiger, 1811)* is the only nocturnal primate genus in Central and South America. The genus is distributed from Panama to the Northeast of Argentina, and from the lowlands of the Andes to the Atlantic coast (Wright, 1981). Eleven species are currently recognized (Fig. 1): *Aotus lemurinus, A. zonalis, A. griseimembra, A. jorgehernandezi, A. brumbacki, A. trivirgatus, A. vociferans, A. miconax, A. nancymaae, A. nigriceps,* and *A. azarae (Rylands, 2001; Rylands and Russell, 2009; Menezes et al., 2010, Fernández-Duque et al., 2013)*. The species *A. azarae* includes the three subspecies *A. a. boliviensis, A. a. infulatus* and *A. a. azarae (Groves, 2005; Ruíz-García et al., 2011, Fernández-Duque et al., 2013)*. The distribution of *A. a. azarae* (Azara's owl monkey) ranges from parts of Bolivia and Paraguay to Northern Argentina. In Argentina, the subspecies is found in the Provinces of Chaco and Formosa (Rathbun and Gache, 1980; Mudry de Pargament *et al.*, 1984; Zunino *et al*,. 1985; Fernández-Duque *et al.*, 2001), where owl monkeys are locally known as “mirikinás”.

INSERT FIGURE 1 HERE

Natural history of Azara’s owl monkeys

Unlike other owl monkey taxa, the subspecies *A. a. azarae* of the Gran Chaco region is cathemeral (Wright, 1989; Arditi, 1992; Fernández-Duque and Erkert, 2006; Fernández-Duque *et al.*, 2010); in other words, it can be active during the night, as well as during the day (Tattersall, 1987). Social groups are small, consisting of an adult pair, one infant, and up to three juveniles or subadults (Huck *et al.*, 2011). Traditionally, those groups were assumed to be family groups in which the male and the female formed a reproductive pair during their

entire life, or a prolonged period of life until the death of one partner (Wright, 1984; Heymann, 2003). However, nearly 25-30% of the individuals in a population studied since 1996 in the Guaycolec Ranch of Formosa Province live as solitary floaters, and this holds for both males and females (Fernández-Duque and Huck, 2013). Generally, such floaters are subadults that have dispersed from their natal groups, or adults that have been replaced from their social group by an intruder (territories are between 4 and 10 ha large, and overlap with the borders of neighboring groups; Wartmann *et al.*, in press). Such replacements occur approximately once every three years at the population level, but reproducing pairs remain stable for an average of nine years (Fernández-Duque and Huck, 2013).

INSERT FIGURE 2 HERE

The reproductive pair reproduces once a year, with a median inter-birth interval of 370 days (Fernandez-Duque *et al.*, 2002). The single offspring is born after a gestation of 120-130 days (Fernández-Duque *et al.*, 2011). The adult male in the group is the main carrier of the infant (Fig. 2) and takes care of it from the second week of its life (Rotundo *et al.*, 2002; Huck and Fernández-Duque, 2012a). IBirths are seasonal, concentrated between October and December (Fernández-Duque *et al.*, 2002). Subadults of both sexes disperse when they are between two and four years old (Huck and Fernández-Duque, 2012b). Although dispersal events can be observed throughout the year, they tend to concentrate around the birth season (Fernández-Duque and Huntington, 2002; Fernández-Duque, 2009). The animals do not show any conspicuous sexual dimorphism (Fernández-Duque, 2011).

20 YEARS OF STUDIES OF AZARA'S OWL MONKEYS IN ARGENTINA

The Owl Monkey Project, a multi-disciplinary program on the Azara's owl monkey of the Argentinean Chaco, started in 1996. One of the main goals of the project has been to

investigate the evolution of social relationships, the monogamous mating system and parental care characteristic of the subspecies. In particular, we have been interested in examining the roles that males and females have in the maintenance of a monogamous social system. Many of the studies have the goal of examining owl monkeys as an approach to understanding the evolution of human behavior, for example with respect to pair bonding and biparental care. Growing from that initial main goal, the project has expanded and over the years has conducted studies on behavior, demography, population biology, genetics, endocrinology and conservation in collaboration with numerous colleagues from provincial, national and international institutions (http://owlmonkeyproject.wordpress.com/about/).

Behavioral Ecology. Studies on the subspecies' behavioral ecology allow us to examine different hypotheses that propose explanations for the evolution and maintenance of monogamy, and the intense male care of offspring that is characteristic of the genus. It has been suggested that in monogamous species, given the relatively high costs to a female of raising and caring for offspring, males may care directly for infants or provide some kind of indirect services to females. The male-care hypothesis predicts that males are more likely to provide infant care when paternity certainty is high (Sheldon, 2002; Kokko and Jennions, 2008). Moreover, it is predicted that in the absence of male care, for example due to replacements, the development and survival of infants may be affected, for example by reducing survival or lowering dispersal age (Emlen, 1995; Emlen, 1997). To evaluate this hypothesis, we have collected over the last sixteen years behavioral data on male-infant interactions before and after paternal replacements; whether the infant was independent or not, and the position of the infant on the individual transporting it (Rotundo *et al.*, 2005; Huck *et al.*, 2011). We have also examined infant survivorship and its possible correlation with the intensity of such care (Huck and Fernández-Duque, 2012a). We found that the male present in the group when an infant is conceived is the genetic father of the infant (Huck *et al.* 2014).

However, when the replacement of male adults occur (Fernández-Duque and Huck, 2013), the new male still provides intensive care to the infant (i.e., 67% of the time the new resident male transported the (unrelated) infant, compared to 80% of the time by the male resident; Fernández-Duque *et al.* 2008; Fernandez-Duque *et al.*, 2009). Additionally, infant survival was not directly affected by adult replacements (Huck and Fernández-Duque, 2012b). Our evidence suggests that female owl monkeys may not be capable or willing to invest more in their current offspring, at least as long as an adult male is present (Huck and Fernández-Duque, 2012a; Huck *et al.* 2014). In one occasion, a female with a dependent infant (younger than a week-old) was replaced by a female intruder, which offered us a natural experiment to evaluate if a female is capable of caring for infants in the absence of a male. The infant did not survive, suggesting that infant survival may be largely dependent on male care (Huck and Fernández-Duque, 2012a).

Demography and population biology. In Argentina, the first reported survey of this sub-species was conducted in the Provinces of Formosa and Chaco (Rathbun and Gache, 1980). Following that first evaluation, different authors estimated population densities in different forest types along the sub-species distribution (Zunino *et al.* 1985; Arditti and Placci, 1990; Brown and Zunino, 1994; Fernández-Duque *et al.*2001). In all cases, the densities were estimated to be higher in the Eastern than in the Western portions of the Province of Formosa (Tab. 1).

INSERT TABLE 1 HERE

Over the years, we have been able to begin exploring the potential relationship between demographic parameters, population biology, the spatial and temporal distribution of food resources and the social organization of the species (van der Heide *et al.*, 2012;

Fernández-Duque and van der Heide, 2013; Fernández-Duque, *in press*). Specifically, we have examined the hypothesis that socially monogamous owl monkey females are distributed in space in a manner that allows them to maximize their reproductive success, given the distribution and availability of resources. Under this hypothesis, one predicts that the reproductive histories of groups and their subsequent demographic characteristic will be related in some manner to the potential and actual access to resources, which in turn is directly influenced by temporal and spatial resource availability. In this theoretical context, we first predicted that there would be no marked differences among home ranges in the spatial distribution and abundance of food resources. Second, we predicted that there would be a relatively even distribution of food in space that prevents the formation of multi-female groups and leads to socially monogamous ones. Third, if home ranges were similar in quality, we predicted that the number of offspring produced in each territory over a 10-yr period should not differ much. This prediction was formulated under the assumption that the number of offspring produced is intimately related to the nutritional status of a female, which in turn is related to food availability. Fourth, if territories had similar amounts of resources, we expected that they should support similar numbers of individuals, which would be reflected in similar groups sizes. Fifth, assuming that the age when individuals disperse from their natal groups could be partially influenced by competition for resources within the group (Fernandez-Duque, 2009), we predicted that the ages at dispersal would not be very different if territories were similar. We have found that the owl monkey territories differ in size, species evenness, stem abundance and density, total basal area, and food species' stem abundance (van der Heide *et al.*, 2012). Still, despite those differences, we found no marked differences among groups in some demographic parameters expected to be associated with territory quality, such as group size, birth rate, age at natal dispersal, and infant mortality (van der Heide *et al.*, 2012). In other words, in our studies we have not found a strong relationship between potential territory quality and long-term demography when considering the whole

territory and all of the foods available across the year (van der Heide *et al.*, 2012). Instead, our studies suggest that owl monkeys occupy territories that provide similar amounts of reliable dry season foods within the core areas. Although access to these core areas may allow them to overcome severe dry season, our findings underscore the difficulties of understanding the potential causal relationships between ecological factors and demographic and life-history parameters (Fernández-Duque and van der Heide, 2013; Fernández-Duque, *in press*).

Reproductive Endocrinology. One of the goals of the project is to understand why male owl monkeys mate in a monogamous relationship, presumably foregoing other reproductive opportunities and often investing heavily in the care of offspring they cannot be certain to have sired. Most information about the hormonal mechanisms regulating biparental care and monogamous social systems has been restricted to studies from captive animals (Dixson, 1982; Mendoza and Mason, 1986; Dixson, 1994; Valeggia *et al.*, 1999). In titi monkeys (*Callicebus moloch)*, for example, the father was shown to be the infant's primary attachment figure, based on raised plasma cortisol levels in the infant, while both adults experienced increased cortisol levels when separated from each other (Mendoza and Mason, 1986). To evaluate the hypothesis that social monogamy may arise if the temporal distribution of female reproductive cycles limits the mating potential of males, we have analyzed fecal samples collected from wild adult females. Our still limited preliminary analyses have shown that female owl monkeys in the Argentinean Chaco have conceptive cycles with an average length of 22±3 days, and with a profile that is similar to other monogamous Neotropical primates such as *Callicebus*; namely that they show the simultaneous rise of estrone-1-glucuronide and pregnenadiol-3-glucuronide during the luteal phase (Fernández-Duque *et al.* 2011). Apart from the strong birth seasonality with the main peak in beginning of October (Fernández-Duque *et al.* 2002), however, we do not yet have sufficient data to verify how synchronous females' receptive periods actually are.

Molecular Genetics. During these years we have conducted numerous studies to examine the genetic structure of the owl monkey population in Formosa. During the last 14 years, we have collected high-quality DNA samples (hair, ear punches, skin biopsies) from 167 owl monkeys in Argentina and we have genetic data on 15 complete social groups. Initial studies investigated the diversity of mtDNA and microsatellite loci of wild animals in Formosa Province compared to three other species of *Aotus* (Babb *et al.* 2011a, b). We found a mean heterozygosity of 0.44 (0.40-0.48) across 13 microsatellite loci that were polymorphic for the wild population (Babb *et al.* 2011a, b). These microsatellite loci exhibited sufficient allelic variation to enable us to make statistical estimates of kinship between any two individuals in our wild population of owl monkeys (Babb *et al.*, 2011a, b) and to conduct paternity analyses that have shown that the owl monkeys of Argentina are the only intensively sampled primate species for which 0% extra-pair paternity has been reported (Huck *et al.*, 2014). Furthermore, molecular examinations of the arginine vasopressin V1a receptor gene (AVPR1A) and the prolactin receptor gene have provided a necessary background on which to begin developing studies to investigate some of the genetic mechanisms possibly underlying the behavioral repertoire of the species (Babb *et al.*, 2010; Babb *et al.*, 2011b; Babb *et al.*, 2013).

***Conservation in Argentina*.** In July 2012 the species was declared a natural monument in the Formosa province (Formosa province law n° 1582). The total distribution area of Azara's owl monkeys in Argentina was estimated to be 39,000 km^2. Of this, the area of suitable habitat is 156 km^2 in the Chaco Province and 654 km2 in Formosa Province (Rathbun and Gache 1980; Zunino *et al.* 1985; Brown and Zunino 1994). However, these areas were estimated more than 20 years ago, based on maps and satellite images. Recently, we found that Azara's owl monkeys were recorded in Vaca Perdida, in the Western part of the province (Juárez *et al.*, in preparation), and Campos *et al.* (2004) also found the species in the Dry Chaco of Paraguay.

These two findings extend the distribution of the subspecies to longitude 61º (Western limit), nearly 200 km further West. These new records, but also the continuous encroachment of agricultural areas for livestock into natural forests, justify a re-evaluation of the distribution, habitat, and area of available habitat for the subspecies in Argentina. New density estimates, together with a refined territorial evaluation, suggest that the existing owl monkey habitat may host an estimate of 18.000 individuals in the province (Juárez, 2012).

The study of the health of wild populations is a fundamental tool for the protection of the animals, especially in fragments, in order to detect potential threats to the animals that follow recent environmental changes. Wild animals are usually exposed to pathogens that are found in their natural environments and live with them in equilibrium. However, environmental changes, induced by humans, can generate stress and reduce these wild animals' resistance, putting them at health risks that may not have existed before. With the objective to evaluate the health status of the owl monkeys at our study site, field veterinarians regularly take blood samples, fecal samples and samples of external parasites. Some preliminary analyses of blood samples using PCR-RFLP and sequencing detected a subgenus of *Leishmania* (*Viannia*) DNA in four individuals (Acardi *et al.*, 2013). Additional eco-epidemiological and parasitological studies are necessary to confirm this finding.

DEMOGRAPHY OF AZARA'S OWL MONKEYS IN TWO DIFFERENT HABITAT TYPES: GALLERY FOREST AND PATCHES FOREST IN FORMOSA PROVINCE

Evaluations of the relationships between the demography and the habitat have identified two factors that notably impact primate populations: the floristic and general habitat structure where the primates live, and the anthropogenic impact on this habitat or the individuals of a population (Struhsaker, 1981; Branch, 1983; Wallace *et al.*, 1998; Cowlishaw and Dunbar, 2000; Chapman and Peres, 2001; Struhsaker, 2008; Pyritz *et al.*, 2010).

Generally, the habitats of highest quality for primates are those with a larger diversity and density of tree species (Dunbar, 1988; Marsh, 2003). This is probably so because primates show a large diversity in their ecological requirements. The ability of primates to take advantage of different habitat types makes forest environments complex systems that can support a large number of individuals. The relationship between primate density and floristic structure is less clear (Chapman *et al.*, 2002). Furthermore, the existence of other variables could affect primate density, such as the presence or absence of predators, or behavioral variables such as intra-specific or inter-specific resource competition (Struhsaker, 2008).

The comparative approach offers a useful tool to examine the relationships between habitat types and anthropogenic impact on the one hand, and the demography of a species on the other. Previous comparisons between different species and genera emphasized the important limitations faced by primates with specialized diets if they have to live in environments that suffer from spatial reductions of areas offering their preferred foods (Mills *et al.*,1993; Marsh, 2003). Studies that examine differences and similarities between populations of the same species have been rare, since demographic long-term studies have been nearly exclusively limited to a single population (Altmann *et al.*, 1985; Rudran and Fernández-Duque, 2003), or to a limited number of groups or communities (Wrangham and Ross, 2008). When the studies are limited to a single sample, it is impossible to distinguish between demographic characteristics that are a consequence of normal ecological parameters in the study population, and the potentially disturbing impacts of human activities.

Habitat types of owl monkeys

Aotus species occupy a large variety of environments (Wright, 1981). In different regions of Central and South-America they can be found at altitudes between 200 and 2,056 m above sea level (Aquino and Encarnación, 1986; Aquino *et al.*, 1990; De Sousa e Silva Jr. and Nunes, 1995; Wallace *et al.*, 2000; Castaño and Cardona, 2005; Fernández-Duque, 2011).

Although the genus is widely present in tropical areas, studies on how these primates utilize their habitat in Peru (Warner, 2002), Venezuela (Castaño and Cardona, 2005) and Paraguay (Campos *et al*,. 2004) suggest that they do not only use primary forests, but also secondary forests and even some forests that have suffered disturbances.

At the extreme Southern end of their continental distribution, in the humid Chaco of Argentina, Azara's owl monkeys inhabit different habitat types within the landscape matrix (Maturo, 2009). In particular, these are gallery forests and naturally fragmented forest 'islands' or patches, that show important differences, for example with respect to floristic composition, fruit availability, proportion of leaves, and phenophases (Placci, 1995; Giménez, 2004). Therefore, the populations of Azara's owl monkeys of the humid Chaco offer ample opportunities for comparative studies on groups that inhabit qualitatively different habitats units within the same macro environment and with different levels of anthropogenic influence. This allows examining the behavioral plasticity of groups that live in different habitat types and their response to different spatial factors. So, the aim of this research is to understand how different social groups in the humid Chaco of Formosa Province are demographically structured in different habitat types (continuous vs. forest patches), and how the possible differences and similarities in group structures are related to spatial factors.

Since 2007, we have been comparing wild social groups of Azara's owl monkeys in these different habitats. The study is conducted in the Estancia Guaycolec (EG), a 25,000 ha private cattle ranch and in the National Park Rio Pilcomayo (PNRP), a 52,000 ha protected area. In each study area, two sub-sets of owl monkey groups could be identified: social groups within the gallery forests (continuous habitat) (EG: n=14; PNRP: n=20), and groups in forest patches (EG: n=16; PNRP: n=14), as well as two potentially different levels of disturbance (i.e., national park, vs. cattle ranch). During all birth seasons between October 2006 and January 2011, we collected information on group size, estimated age of individuals, and infant

presence from social groups in EG and PNRP. Additionally, we measured the spatial distances between forest patches and gallery forests.

To locate groups in the control area, we walked through the forest at dawn and at dusk when owl monkeys were consistently active. Most of the time we first detected the monkeys through the noises they made while moving, but then we took advantage of ambient light at dawn and dusk to count individuals and assess relative body size. For our study, we used a method that had not previously been used for *Aotus*. Our method combines previous knowledge of the sub-species, the use of playbacks, and tools of classical field methods used to study diurnal primates (Setchell and Curtis, 2003), in order to minimize errors and optimize the sample for these cathemeral primates. When we were unsuccessful locating them, we sometimes played hoot calls (Moynihan, 1964; Wright, 1981, Wright, 1989), a low-pitch, relatively loud vocalization that is extremely effective in attracting individuals (Depeine *et al.*, 2008). The mapping of territories is one of the most reliable methods used for density estimations of Neotropical primates (Janson and Terborgh, 1985; Rudran, 1979; Ojasti, 2000). We stayed with each group for as long as they remained active in the morning, usually a few hours, or until it was too dark to reliably see at dusk. While following them, we recorded their positions with a GPS. The strict territoriality of owl monkeys and the relatively small overlap that exists among territories make it possible to recognize different groups via a combination of spatial data and group composition data (Fernandez-Duque *et al.*, 2008; Wright, 1978). It is extremely difficult to sex owl monkeys in the field, as there is no obvious sexual dimorphism in body size or fur patterns, and the testes are relatively small (Dixson *et al.*, 1980). We were able to sex some individuals when the female was lactating and the nipples were prominent, or if we were close enough to observe the testes. Otherwise, we assumed that there was one adult male and one adult female in each group. To classify individuals in age categories we used a combination of demographic, behavioral, and morphometric data. We estimated age based on: 1) width and length of the dark stain produced by the subcaudal gland secretion, 2)

relative body size, 3) presence of prominent nipples, and 4) behavioral patterns. Adults were the largest individuals in the group, and also had visually conspicuous subcaudal secretions on the ventral side of their tail (Dixson *et al.*, 1980). We also classified an individual as adult if we observed it nursing or transporting an infant because infant carrying by non-adults is extremely infrequent (Fernandez-Duque *et al.*, 2008). We classified individuals as juveniles if they were smaller than the adults in the group and showed some staining of the ventral side of their tail due to perianal secretions. Finally, we classified individuals as infants when they were the smallest individuals in the group, had no stains on the tail, and were carried by an adult when moving between trees. To compare the age structure in both areas we limited our analyses to three categories: infants, juveniles, and adults.

We compared group sizes in the both areas with a Mann-Whitney U-test for two independent samples.

Results and discussion

The results of our investigations confirm that the estimated individual densities (i.e., total number of individuals per ha) for the private ranch (EG) are higher than in the National Park (PNRP). In contrast, parameters like size and range of groups, birth rates and age were similar between sites (Tab. 1). This heterogeneity in density of the subspecies had already been mentioned in various studies conducted in the Formosa Province (Rathbun and Gache, 1980; Zunino *et al.*, 1985; Brown and Zunino, 1994), and these new results confirm the conclusions by these authors, even though different methods were employed (Tab. 2).

INSERT TABLE 2 HERE

The individual density of Azara's owl monkeys in gallery forests in the EG were high compared to the estimates that exist for the subspecies *A. a. azarae* (33.2 ind/km^2; Svensson,

2008). The situation in PNRP is somewhat different, with a slightly lower individual density than the overall mean (Tab. 1). Svensson (2008) compared different study methods that had been used for calculations of density estimates for different *Aotus* species and found that transect censuses over estimated group densities. By incorporating a new methodological tool that is efficient (playbacks), we have implemented a field schedule that takes the lunar cycle, the birth seasonality, and the territoriality of these primates into account in order to estimate individual densities. These densities are high, even when compared to other species like *A. nancymaae* (31.8±18.6 ind/km^2; Aquino and Encarnación, 1986; Maldonado Rodríguez, 2011) and *A. nigriceps* (38 ind/km^2; Wright, 1985).

The results confirm that group sizes, birth rates, and individual and group densities were larger for gallery forests than for forest patches at both study sites (Tab. 2). We found similarities in birth rates between different habitat types in PNRP, and in age structure at both study sites. These results coincide with various studies that suggest that in environments of lower quality, like forest patches, the population demography can be notably changed (e.g., the lower number of species of primates in patches, low density, lower birth rates, high mortality rates; Janson and Chapman, 1999; Di Fiore *et al.*, 2006; De Moura, 2007; Pyritz *et al.*, 2010). The results of the density estimation in forest patches (rather than gallery forest) at both study sites show that they are lower than the mean value from all other studies on that species (22.4 ±18.6; Svensson, 2008) and are similar to densities observed for *Aotus zonalis* in remaining forest fragments of Panama (18.4 ind/km^2; Svensson, 2010).

The quantitative evidence for smaller group sizes in forest patches opens up numerous questions. It has been suggested that food availability is lower in forest patches (with low availability of fruits and leaves in both the dry and humid season, Giménez, 2004) compared to gallery forests. This, in turn, could result in higher mortality rates in forest patches than in gallery forests (Estrada and Coates-Estrada, 1996; Marsh, 2003). Nevertheless, it was observed that the range of group sizes was not very different compared to groups in gallery

forests, since in all cases group sizes ranged between 2-5 individuals, but the mean number of individuals was lower in the forest patches (Tab. 2). These smaller group sizes could be a reflection of the health status of the animals, and might also be related to the lower birth rates that we observed for groups in the forest patches in EG. This needs to be further studied in order to understand the population dynamics of groups in forest patches. It is of paramount importance to evaluate to what degree mortality, emigration rates, and the health status of the animals influence the demographic structure of the owl monkeys in such habitat types, since these areas are more affected by agriculture and cattle farming than the gallery forests.

Before the onset of this study comparing the different habitats, a clear association had been expected between the presence or absence of Azara's owl monkeys in forest patches and certain spatial factors that had originally been judged to be important (*e.g.*, vegetation structure, degree of isolation, and the surface of the island in ha). We were able to study 73 forests patches in the two areas (EG=38 and PNRP= 35 forest patches). In EG, 53% of the patches were smaller than 4 ha (n=20), while in the PNRP, 46% were that small (n=16). A logistic model predicted a 90% probability of finding monkeys in forests patches with an area of 11.4 ha, and with a 50% probability if the area was between 5 and 6 ha. At least once, we found owl monkeys in one island with an area of only 0.86 ha. Our results confirmed that although monkeys can be found in patches smaller (range=0.1-3.9 ha; Juárez, 2012) than the smallest territory size recorded for groups in gallery forests (4-10 ha; van der Heide *et al.* 2012; Wartmann *et al.* 2014), the proportion of such patches actually containing owl monkey groups was low.

The fact that Azara´s owl monkeys can be found in forests patches smaller than the normal territory sizes of groups living in gallery forests suggests a certain plasticity of the sub-species to inhabit spaces of a relatively inferior quality such as the natural patches of shrubs or “algarrobales” that have a larger amount of species such as *Prosopis, Acacia caven* or *Geoffroea decorticans* than other forest patches (Juárez, 2012). There is only information

available on the use of forest patches for *Aotus lemurinus* in Venezuela (Castaño and Cardona, 2005), and in Bolivia for *A. azarae (Wallace et al., 1998),* where they were found to inhabit anthropogenically fragmented patches of variable sizes (1.5 to ≥2000 ha). Group sizes for these two species were similar, with 2-5 individuals. Although the genus *Aotus* has a wide geographical distribution that includes wide areas of Amazonian forests under the process of fragmentation (De Carvalho Jr., 2003), there is little information on basic aspects of their population ecology in fragmented habitats. Defler (2003) has reported some plasticity in *A. lemurinus* individuals who can live in forests with a certain degree of alteration. Svensson (2008) also mentions this potential plasticity given her observations of *A. zonalis* in primary and secondary forests. Castaño and Cardona (2005) confirm this for different types of landscape matrices including forests fragments immersed in cattle farming land, surrounded by grazing land and coffee plantations, deforested areas, and forest contaminated with trash. These authors have preliminarily reported movements of individuals between these small forest fragments (Castaño and Cardona, 2005).

The movement between forests patches is an important factor affecting the survival of these animals. A local example of such movements between forest patches was documented by an accident: an Azara's owl monkey was hit by a tractor moving in the savanna between forest patches in the PNRP (pers. Com. Matías Carpinetto, Director of the PNRP). Another example for *A. zonalis* is cited by Castaño *et al.* (2010), with the direct observation of animals moving on electric power lines and through isolated trees in order to move from one patch to the next.

Although these are anecdotes, they exemplify that two species of the same genus with widely different geographic ranges (*A. zonalis* and *A. azarai*) have the ability to survive in disturbed and fragmented environments. The subspecies clearly shows the capacity to colonize places distant from continuous habitats, as shown in this study. In EG the distances between forests patches and gallery forests ranged from 20 and 3200 m; in PNRP this range

was 3100-12500m. Our logistic model suggests that the distance to gallery forests or to continuous humid Chaco forest had no apparent influence on the presence or absence of monkeys in the forests patches ($B_{gallery\ forest}$=-0.001; et.=0.000; X^2 *Wald*=2.3; p=0.123). This raises the question of how owl monkeys use the matrix in fragmented landscapes. Dense palm trees, although they are not characterized as a habitat for Azara's owl monkeys, could be used as sleeping sites, additional resources and as bridges between inhabitable environments and function as corridors or "stepping trees" between forests patches. Such dense palm trees grow naturally in the humid Chaco, and eventually density increases in anthropogenically affected environments (e.g., through the use of fire, Neiff *et al.*, 2004). It is necessary to continue our studies in this environment to understand the variables that can influence the habitat use of Azara´s owl monkey in the humid Chaco.

CONCLUSIONS

Our long-term study on the owl monkeys of the Argentinean humid Chaco does not only continue to contribute to the understanding of the behavior and the ecology of this species, as well as the evolution of social monogamy and male care, but it also provides important information on the demography and habitat use of a species that has recently been declared a Natural Monument in Formosa province.

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773Fig. 1: Geographical distribution of the genus *Aotus* in Central and South America (map from
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775
776Fig. 1: Distribución geográfica del género *Aotus* en América Central y del Sur (mapa extraído
777de Menezes *et al.,* 2010).
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Fig. 2: Adult male Azara's owl monkey carrying an infant (photo: V. Dávalos/Proyecto Mirikiná, Formosa, Argentina).

Fig. 2: Macho adulto de mono mirikiná cargando dorsalmente un infante (foto: V. Dávalos/Proyecto Mirikiná, Formosa, Argentina).

Table 1: Group and individual densities, and group sizes for *Aotus a. azarai* in different habitat types in Argentina (na: no data available; c: census; be: behavior and ecology study).

Tabla 1: Densidad grupal e individual y tamaño de grupo para *Aotus a. azarai* en diferentes hábitats en Argentina (na: datos no disponibles; c: censos; be: estudios de ecología y comportamiento).

Table 2: Demographic parameters of social groups in two habitat types: gallery forest and forest patches in Guaycolec Ranch (EG) and Pilcomayo National Park (PNRP), Argentina.

Tabla 2: Parámetros demográficos de grupos sociales en dos tipos de hábitats: selvas en galería e isletas de bosques en la Estancia Guaycolec (EG) y en el Parque Nacional Río Pilcomayo (PNRP), Argentina.